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With a little help from my friends: Community facilitation increases performance in the dwarf shrub *Salix herbacea*

J.A. Wheeler[a,b,*], F. Schnider[a], J. Sedlacek[c], A.J. Cortés[d], S. Wipf[a], G. Hoch[b], C. Rixen[a]

[a] *WSL Institute for Snow and Avalanche Research SLF, 7260 Davos, Switzerland*
[b] *University of Basel, Institute of Botany, 4056 Basel, Switzerland*
[c] *University of Konstanz, Department of Biology, 78457 Konstanz, Germany*
[d] *University of Uppsala, Evolutionary Biology Centre, 752 36 Uppsala, Sweden*

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Abstract

Shifts between positive and negative plant interactions along environmental stress gradients can affect alpine plant performance. We removed neighbours around *Salix herbacea*, a common arctic and alpine dwarf shrub, along elevational and snowmelt gradients on three mountains in Switzerland. The objectives of our study were to determine the effect of neighbours on phenological, morphological, and fitness traits of *S. herbacea*, and to determine whether neighbour interactions shift from competition to facilitation along environmental stress gradients.

Target plants without neighbours required less time for fruit production; however, they also were more likely to be damaged by caterpillar herbivory. Effects of neighbour removal changed along the environmental gradients: plants without neighbours had smaller leaves on earlier snowmelt sites, and increased fungal damage with increasing elevation. Without neighbour removal, damage generally led to reduced female flowering under later snowmelt conditions in the following summer.

Our results indicate that the majority of neighbour interactions influencing *S. herbacea* are facilitative, particularly at stressful early snowmelt and high elevation sites. We suggest that neighbours moderate environmental conditions by protecting plants from temperature extremes, and reduce plant apparency to caterpillars. Neighbours also indirectly increase fitness by reducing damage. Facilitation by neighbours may become more important under climate change, as early snowmelt may increase stress.

Zusammenfassung

Verschiebungen zwischen positiven und negativen Pflanzeninteraktionen entlang von abiotischen Stressgradienten können sich auf Wachstum und Fortpflanzung von alpinen Pflanzenarten auswirken. Entlang von Gradienten von unterschiedlichen Höhenstufen und Zeitpunkten der Schneeschmelze an drei Bergen in der Schweiz entfernten wir Nachbarpflanzen der Krautweide *Salix herbacea*, eines in alpinen und arktischen Gebieten weit verbreiteten Zwergstrauches. Unsere Studie hatte zum Ziel, die Wirkung von Nachbarpflanzen auf phenologische, morphologische und Fitness-Merkmale von *S. herbacea* zu untersuchen und herauszufinden, ob Interaktionen mit den Nachbarspflanzen entlang von umweltbedingten Stressgradienten zwischen negativ (Konkurrenz) und positiv (Facilitation) variieren.

*Corresponding author. Current address: Department of Environmental Conservation, University of Massachusetts, Amherst, MA, USA. Tel.: +1 413 545 3114; fax: +1 413 545 4358.
E-mail address: juliawheeler@eco.umass.edu (J.A. Wheeler).

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Salix herbacea ohne Nachbarn brauchten weniger Zeit zur Produktion von Früchten; jedoch hatten diese Pflanzen ein erhöhtes Risiko, von blattfressenden Raupen befallen zu werden. Das Entfernen der Nachbarpflanzen zeigte unterschiedliche Effekte entlang der Umweltgradienten: Es führte zu einer kleineren Blattgröße an Standorten mit früherer Schneeschmelze und zu erhöhtem Schaden durch Pilze mit zunehmender Höhenlage. Weibliche Pflanzen mit Blattschäden bildeten im folgenden Sommer an Standorten mit später Schneeschmelze generell weniger Blüten.

Unsere Ergebnisse zeigen, dass ein Großteil der signifikanten Interaktionen mit Nachbarpflanzen für *S. herbacea* positiv sind, besonders an extremen Standorten mit früher Schneeschmelze und in großer Höhe. Wir folgern, dass Nachbarpflanzen Umweltbedingungen abmildern, indem sie Pflanzen vor Temperaturextremen schützen und die Wahrnehmbarkeit durch Raupen vermindern. Nachbarpflanzen erhöhen auch indirekt die Fitness von *S. herbacea*, indem sie Blattschäden reduzieren. "Facilitation" durch Nachbarpflanzen könnte unter sich verändernden klimatischen Faktoren eine zunehmend wichtige Rolle für *S. herbacea* spielen, da eine frühere Schneeschmelze zu erhöhtem Stress führen könnte.

Keywords: Plant–plant interactions; Early snowmelt; Alpine shrubs; Neighbour removal; Stress gradient hypothesis; Snowmelt gradient; Elevation gradient

Introduction

In temperate alpine ecosystems, plant communities are strongly structured by the effects of abiotic conditions, such as growing season temperatures and snowmelt timing. Heterogeneous microtopography controls snowmelt, temperatures vary with elevation, and both are important drivers of structure and function in local alpine plant communities (Körner 2003). However, plant–plant interactions also shape the structure and function in alpine plant communities (Soliveres & Maestre 2014), and these neighbour interactions are often strongly influenced by environmental conditions (Brooker 2006; Schöb, Armas, Guler, Prieto, & Pugnaire 2013).

Bertness & Callaway (1994) first predicted that under the stress gradient hypothesis, net plant–plant interactions are generally expected to shift from primarily competitive in productive (or low-stress) habitats, to primarily facilitative in low-productivity (or high-stress) habitats (e.g., Bertness and Callaway 1994; Choler, Michalet, Callaway 2001; Brooker 2006). In alpine ecosystems, many studies have documented shifts from competition to facilitation interactions along environmental stress gradients, such as elevation and moisture (e.g., Callaway et al. 2002; Badano, Villarroel, Bustamante, Marquet, & Carieres 2007; Schöb et al. 2013; Grassein, Lavorel, & Till-Bottraud 2014). Studies examining neighbour interactions along snowmelt gradients are rarer (but see Wipf, Rixen, & Mulder 2006; Schöb et al. 2010), and few if any studies examine the importance of, and the shift in, neighbour interactions along elevational and snowmelt gradients simultaneously.

Higher elevation and early snowmelt microhabitats may be stressful for many alpine plant species due to lower temperatures during the early growing season and a higher likelihood of damaging frost events (Inouye 2008; Wheeler et al. 2014). Further, early snowmelt can be associated with higher incidences of insect herbivory and phytopathogens (Roy, Gusewell, & Harte 2004, Wheeler et al. unpublished). In these stressful microhabitats, neighbours can form a microclimate that deviates from ambient conditions: canopies can shelter smaller plants from temperature extremes, alter snow accumulation, and increase nutrient enrichment through increased litter fall (e.g., Callaway 1995; Cavieres, Badano, Sierra-Almeida, & Molina-Montenegro 2007). Further, neighbours can shelter plants from insect herbivores through concealment or associational resistance (e.g., Callaway 1995; Schöb et al. 2010; Castagneyrol, Giffard, Pere, & Jactel 2013).

Salix herbacea L., a common dioecious arctic/alpine dwarf shrub and S-strategist (Grime 1997), represents an excellent species for studying neighbour interactions along both elevational and snowmelt gradients; in the eastern Swiss Alps, it covers a long elevational gradient (~800 m) and grows in a wide range of snowmelt microhabitats, from early-exposure ridges to late-lying snowbeds. Past work on *S. herbacea* has indicated that fitness may be reduced and exposure to frost, herbivory and phytopathogen damage will increase under early snowmelt scenarios, and missing positive soil feedbacks may constrain migration beyond its current range (Sedlacek, Bossdorf, Cortés, Wheeler & van Kleunen; Wheeler et al. 2014; Wheeler et al. unpublished). Further, *S. herbacea* demonstrates strong plastic responses to changes in snowmelt conditions in leaf size and phenology (Sedlacek et al., unpublished). High gene flow has led to low genetic differentiation between local populations (Cortés et al. 2014).

Our objectives were (1) to examine the direct and indirect effects of neighbour interactions on phenological and morphological traits, fitness proxies and damage in *S. herbacea*, and when neighbour interactions were influential, (2) to determine if interactions shift from competitive to facilitative along increasing stress gradients. Since *S. herbacea* is a long-lived species, we hypothesize that plant–plant interactions will have the strongest effect on strongly plastic traits that can respond rapidly to changes in competition or facilitation intensity, such as leaf size. We also hypothesize that